Chapter 15

Notes on the Bats of the Réserve Naturelle Intégrale d'Andohahela and Surrounding Areas of Southeastern Madagascar

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Abstract

Four bat species were collected in the Réserve Naturelle Intégrale d'Andohahela: *Rousettus madagascariensis, Miniopterus manavi, Mormopterus jugularis,* and *Myotis goudoti.* With the exception of *Mormopterus,* all were obtained in the humid forest portions of the reserve (parcel 1); *Mormopterus* was netted in an area of spiny bush vegetation (parcel 2). The humid forest species are broadly distributed across the island and occur in both forested and disturbed areas. An analysis of the forest-dwelling bat faunas known from several eastern humid forest sites indicates that species richness is low and that there is little change in the community across this region, which covers about 12° of latitude.

Résumé

Quatre espèces de chauves-souris ont été collectées dans la Réserve Naturelle Intégrale d'Andohahela: *Rousettus madagascariensis, Miniopterus manavi, Mormopterus jugularis,* et *Myotis goudoti.* A l'exception du *Mormopterus,* on les a toutes prises dans les zones de forêts humides de la réserve (Parcelle 1), et le *Mormopterus* a été attrapé par filet dans une zone de végétation broussailleuse et épineuse (Parcelle 2). Les espèces de forêt humide sont largement éparpillées à travers l'île aussi bien dans la région boisée et dans la région perturbé. Une analyse effectuée sur les chauves-souris demeurant dans la forêt, connue dans plusieurs sites de forêt humide à l'Est a indiqué que la richesse des espèces sont faible et qu'il y a presque aucun changement au niveau de cette communauté à travers la région qui couvre presque 12° de latitude.

Introduction

Peterson et al. (1995) recently published a monograph on the Chiroptera of Madagascar that provides one of the most important summaries of the island's bat fauna since it was treated by Dorst (1947a,b, 1948). Although the monograph is based on original fieldwork and a review of previous collections in museums, remarkably few ar-

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eas of the island have been worked for bats, and data on the natural history and distribution of most species remain rudimentary. Furthermore, a considerable amount of new information has been collected since the monograph was completed.

Species lists on the bat faunas that occur in the majority of Madagascar's reserves are not available (Nicoll & Langrand, 1989); such basic information on local species is important for management purposes. Recent bat surveys conducted within protected areas such as the Réserve Naturelle Intégrale (RNI) d'Andringitra, RNI de Ma-

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rojejy, Réserve Spéciale (RS) d'Anjanaharibe-Sud, and the Parc National (PN) de Zombitse et Vohibasia are starting to fill this void (Pont & Armstrong, 1990; Rasolozaka, 1994; Goodman, 1996, 1998). Although bat netting was not a major activity during our inventory of the RNI d'Andohahela, data on the few bats that were captured are presented here. Information is also presented on the regional bat fauna, and distributional patterns of forest-dwelling species across the eastern humid forest are briefly summarized.

Materials and Methods

At each of the inventory sites along the elevational transect in the humid forest of parcel 1 and the single site in the spiny bush of parcel 2 (see Chapter 1), 10 mist-nets (12 m long \times 2.6 m high) were erected for 5-day periods as a standardized means of capturing birds (see Chapter 12; Goodman et al., 1997). In all cases nets were placed in the forest understory, with the lowest rung close to or touching the ground. A few bats were collected in the bird nets. Nets were also set up at several sites with the specific intent of capturing bats; these were generally placed across streams or small rivers. Bat nets were attended from dusk to 2000 hr and checked several times during the night.

Netted bats were prepared as specimens that are deposited in the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale (UADBA), Université d'Antananarivo, Antananarivo. Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UAD-BA-SMG). Most of the bats were prepared as fluid-preserved specimens, and information is not available on internal reproductive organs or skull measurements. Information is also presented on a small collection of bats made in the Tolagnaro area, including in and around the RNI d'Andohahela, by G. Ken Creighton in 1989 and 1990. This collection is housed in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. The systematic arrangement used by Peterson et al. (1995) is followed here.

Measurements

Measurements were made from animals in the flesh and from prepared crania. The abbreviations and definitions for measurements (all in mm, with the exception of WT) follow.

- BBC breadth of braincase: distance measured across the hamular processes of the squamosal at the point where they border the mastoid bullae
- CM canine-molar length: measured from anterior alveolar border of canine to posterior alveolar border of last molar
- EL ear length: measured from base of the ear (notch) to the distalmost edge of the pinna
- FA forearm length: measured from outside edge of the wrist to outside edge of the elbow (with wing folded)
- HF hind foot length: measured from the back edge of the heel to the end of the longest toe (not including claw)
- IOB interorbital breadth: the minimum distance across the frontal bones between the orbits. In Megachiroptera this was taken in front of the postorbital processes; in Microchiroptera it was taken behind them
- ML mandible length: measured from midpoint of mandibular condyle to anteriormost point of dentary
- ONL occipitonasal length: distance between tip of the nasals and posteriormost edge of the occiput, just above the foramen magnum
- TL tail length: measured from base of tail (at right angles to the body) to end of the distalmost vertebra
- TOTL total length of body and tail: measured from nose tip to end of the distalmost tail vertebra
- TR tragus length: measured from base of tragus to the distalmost tip
- WC width across canines: measured across the exteriormost alveolar base of the upper canines
- WT weight: measured in grams (g) with Pesola spring scales. Animals ≤10 g were weighed to the nearest 0.1 g; those between 11 and 100 g were weighed to within 0.5 g

zygomatic breadth: greatest distance between the lateral surfaces of the zygomatic arches.

Species Accounts

ZB

Family Pteropodidae

Rousettus madagascariensis Grandidier, 1929

Fifteen individual *Rousettus madagascariensis* were captured at 400 m in a net spanning the Andranohahela River. Most of these individuals were taken early one morning before dawn as they were flying up the river valley. The site was surrounded by intact lowland humid forest and located in a valley below the high peaks of the Anosyenne mountain chain. Upland areas of this region contain numerous rocky outcrops with a variety of nooks and crannies that would provide ideal roosting places for this bat. Lowland areas outside the reserve are largely made up of open agricultural lands. This bat feeds extensively on the fruits of banana (*Musa*, family Musaceae) and litchi (*Litchi chinensis*, family Sapindaceae).

In mid-November 1989 at a site 2 km WNW of Tolagnaro, near the base of Pic St. Louis and in a grove of litchi trees with ripening fruit, Ken Creighton and S.M.G. netted well over 30 Rousettus madagascariensis during one night with two standard 12 m mist-nets. The specimens are housed in the USNM. These fruit bats would grasp a ripe fruit in their mouths and fly off to consume it. Rousettus madagascariensis has also been netted in parcel 3 of the RNI d'Andohahela (M. Pidgeon, pers. comm.), in the Nahampoana Forest (USNM 577059-577061, 577250-577255), and in the dry littoral forest near Petriky (USNM 578724). It has also been reported from a site 30 km NE of Tolagnaro (Peterson et al., 1995). Measurements of R. madagascariensis from the RNI d'Andohahela (Table 15-1) fall within the ranges given by Bergmans (1994) and Peterson et al. (1995) for this species.

REPRODUCTION—The individuals netted in the RNI d'Andohahela represented a variety of age classes, from young individuals with partially unfused finger joints, to adult males and females that were not in reproductive condition, to males with large scrotal testes and pregnant females. Three females were pregnant with young; two of these individuals were adults, with embryos measuring 30 mm crown-rump length, and the third was a subadult (based on skull ossification), with a single embryo measuring 17 mm crown-rump length.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 8 km NW of Eminiminy, 440 m (FMNH 156495–156498, 156606–156611, UADBA-SMG 7405, 7407, 7410, 7415, 7416).

Family Hipposideridae

Hipposideros commersoni commersoni (E. Geoffroy, 1813)

This species was observed on two occasions in the humid forest portion of the reserve—in the 400 m and 810 m transect zones during night walks in the forest. No individual was captured in the mist-nets. It has been collected in the littoral forest of Manafiafy, north of Tolagnaro (USNM 578738, 578855).

Family Vespertilionidae

Myotis goudoti goudoti (A. Smith, 1834)

Two *Myotis goudoti* were netted in the humid forest of parcel 1. One was captured at dusk in a mist-net placed over a small tributary of the Andranohahela River at 810 m in an area surrounded by transitional lowland/montane forest. The second individual was netted at dusk in a net placed on a ridge crest in primary montane forest at 1200 m. The latter record is apparently rather high for this species, which has generally been collected in lowland areas up to about 800 m (Goodman, 1996). Measurements of these two specimens are presented in Table 15-1.

Several other records of *Myotis goudoti* from the region include the littoral forests of Manafiafy (USNM 578740, 578741) and Mandena (USNM 578739, 578854) and sites on lateritic soils such as the Marovony Forest at 30 m (USNM 577069), Manantantely Forest at 60 m (USNM 577066), and the Nahampoana Forest between 100 and 450 m (USNM 577067, 577068, 577259, 577260, 577262–577264). It has also been collected in transitional and dry forests associated with riverine habitat near the Itaranta River (USNM 577070, 577071) and along the Anosy River near Bevilany (USNM 577261).

REPRODUCTION-One specimen was a male with

		TABLE 15-1. Sele	cted measuremen	ts of bats collec	ted during the su	rvey.			
Species	Age	TOTL	TL	HF	EL	TR	FA	WT	
Rousettus madagascariensis	adult (n = 12)	124.0 ± 4.2	12.5 ± 2.2 0-15	15.3 ± 0.2 14.16	18.6 ± 1.0		69.7 ± 3.2 62.74	53.1 ± 17.4 $41.5_71.5$	
	$\sin - \frac{12}{2}$	118.3 ± 2.3	12.3 ± 0.6	14.7 ± 0.6	18.7 ± 0.6		69.3 ± 1.5	49.3 ± 1.5	
Myotis goudoti	(c - n) adults	11/-121	49, 39	8, 7	15, 16	6.5, —	40, 37	40.3-31.3 8.2, 5.2	
Miniopterus manavi	adults	97, 92	42, 46	7, 7	10, 10	6, 6	37, 38	5.3, 8.0	
Mormopterus jugularis	(々、キ) adults (22)	115, 103	26, 31	7, 7	21, 18	[37, 37	12.5, 11.0	
			TABLE 15-1.	Continued.					
Species	Age	ONL	ZB	IOB	BBC	WC	CM	ML	1
Rousettus madagascariensis	adult $(n = 5)$	34.3 ± 1.9 31.0-35.9	21.0 ± 1.7 18.1-22.6	6.8 ± 0.6 6.0-7.4	14.4 ± 0.7 13.5-15.1	7.1 ± 0.5 6.3-7.6	13.4 ± 0.9 12.3 - 14.3	27.8 ± 1.7 25.1-29.2	
Myotis goudoti	subadult adult (2)	33.7 14.2	19.2 9.4	6.0 3.1	14.3 7.0	4.0	13.0 5.8	11.0	
Miniopterus manavi	adults (δ, φ)	13.1, 13.4	7.0, 7.2	3.2, 3.1	6.8, 7.0	3.8, 3.9	5.2, 5.2	10.1, 10.1	
Mormopterus jugularis	adults (¥ ¥)	15.4, 15.5	10.0, 10.1	3.8, 3.6	8.3, 8.1	4.4, 4.4	5.8, 5.8	11.4, 11.6	

Descriptive statistics are as presented mean ± standard deviation and range, and the number of specimens. With the exception of wt (weight, in g), measurements are in millimeters. See text (p. 252) for explanation of abbreviations.

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abdominal testes; the other was a female with an open pubic symphysis and large mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 12.5 km NW of Eminiminy, 810 m (FMNH 156499); parcel 1, 13.5 km NW of Eminiminy, 1200 m (FMNH 156500).

Miniopterus manavi Thomas, 1906

Two individuals of this species were obtained in parcel 1 of the RNI d'Andohahela. One was netted at 810 m within 10 min after dusk over a small tributary of the Andranohahela River. The bare skin around the eye was dull yellow. The second individual was found by A. Raselimanana at 1500 m in a night roost under a small rock overhang. These specimens are assigned to Miniopterus manavi on the basis of differences in measurements of Malagasy Miniopterus spp. outlined by Peterson et al. (1995) and Hill (1993). Miniopterus manavi has also been collected in the Marosohy Forest near the northern limit of the reserve (parcel 1) at about 350 m (USNM 578744, 578745). It has also been reported along the Mandromodromotra River, 16 km NE of Tolagnaro (Peterson et al., 1995) and near Tolagnaro (Hill, 1993). In the USNM there are series of this species taken at other sites in southeastern Madagascar that include the Nahampoana Forest, 7 km NNW of Tolagnaro, between 100 and 450 m 577102-577119, (USNM 577129-577131, 577297-577299, 577302-577307); the Manantantely Forest, 8-12 km WNW of Tolagnaro, between 100 and 450 m (USNM 577096-577101, 577296); the Itapera Forest, approximately 21 km NW of Tolagnaro, and near sea level (USNM 577128); and along the Itaranta River, 20 km WNW of Ranopiso, at 20 m (USNM 577120-577122, 577124, 577125).

REPRODUCTION—The male had slightly descended scrotal testes, and the female had large mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 12.5 km NW of Eminiminy, 810 m (FMNH 156501); parcel 1, 15.0 km NW of Eminiminy, 1500 m (FMNH 156502).

Family Molossidae

Mormopterus jugularis (Peters, 1865)

Two individuals of *Mormopterus jugularis* were netted over a small river at the edge of par-

cel 2 of the RNI d'Andohahela. On one side of the river was heavily degraded gallery forest and on the other bank slightly degraded spiny bush. *Mormopterus jugularis* has also been collected in the humid portion of southeastern Madagascar north of Manantenina (USNM 577161–577172, 577178–577188) and in drier areas near the Itaranta Forest (USNM 577132–577134), near Beraketa (USNM 577361), and in the Ankapoky Forest (USNM 577313, 577314, 577321, 577322, 577336). This species has a broad distribution across the island and generally roosts in buildings (Peterson et al., 1995).

REPRODUCTION—The two individuals captured were females, one with large mammae and the other with slightly enlarged mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 2, 7.5 km ENE of Hazofotsy, 120 m (FMNH 156612, 156613).

Other Regional Records

Several other species of Megachiroptera and Microchiroptera bats have been reported or collected in the Tolagnaro area and around the various parcels of the RNI d'Andohahela. The holotype of Pteropus rufus princeps, a subspecies not currently recognized, was collected in the Tolagnaro region (Andersen, 1908). This species has been found near Tolagnaro (Peterson et al., 1995), Bemangidy (USNM 317901, 317902), and Manantenina (USNM 578832, 578833). Colonies are also known from Berenty along the Mandrare River (Nicoll & Langrand, 1989) and in the Manafiafy (St. Luce) forest (Goodman, pers. obs.). Eidolon dupreanum has been reported from the Tolagnaro region and the Grotte d'Andrahomana, along the coast south of Ranopiso (Peterson et al., 1995).

Among the Microchiroptera several other species have been reported from the region. *Myzopoda aurita*, a member of the endemic family Myzopodidae, was obtained at Antanifotsy, 8 km N of Tolagnaro (Göpfert & Wasserthal, 1995); 4 km SSE and 2–3 km NW of Manafiafy (USNM 578742, 578743, 578856–578858); along the Mandromodromotra River, 15 km NE of Tolagnaro (Peterson et al., 1995); near Bemangidy (FMNH 85237, 92832, 92833); and in the Analalava Forest (USNM 577065). The Bemangidy specimens were found "in curled-up central leaf of very large traveller's palm [*Ravenala mada*-

	Site, latitude, and elevational range sampled				
Species	Andohahela* 24°36′S 400–1875 m	Andringitra† 22°13′S 720–1625 m	Anjanaharibe-Sud‡ 14°45′S 875–1950 m	Marojejy¶ 14°26′S ∼500–700 m	
Rousettus madagascariensis	+	+	+	+	
Emballonura atrata				+	
Hipposideros commersoni	+	+			
Triaenops rufus				+	
Myotis goudoti	+	+	+	+	
Scotophilus robustus				+	
Miniopterus fraterculus			+		
Miniopterus manavi	+				
Miniopterus minor		+			
Miniopterus spp.				+	
Myzopoda aurita				+	
Tadarida pumila				+	
Total number of species	4	4	3	8	

TABLE 15-2. A comparison of the forest-dwelling bat faunas of several sites in the eastern humid forests of Madagascar.

* Restricted to the humid forest portions of the reserve and based on information presented in this chapter.

† Goodman (1996).

‡ Goodman (1998).

¶ Pont and Armstrong (1990).

Apparently several different species were netted and no voucher specimens were collected. Field determinations for this genus are unreliable.

gascariensis, family Strelitziaceae] near river" (H. Hoogstraal, field notes, FMNH). The horseshoe-shaped pads on the sole and thumb apparently aid this species in moving along and clinging to the leaves. At numerous other sites on the island Myzopoda has been captured in heavily degraded areas and at the edge of marshes where Ravenala is a dominant species (Schliemann & Maas, 1978; Göpfert & Wasserthal, 1995). There is some evidence, however, that Ravenala is not the only plant used for roost sites. I captured two of the USNM specimens from Manafiafy mentioned above at dusk in mist-nets placed at understory level and within relatively intact littoral forest. These nets were at least 500 m from any Ravenala, and it was my impression that the individuals were leaving a nearby roosting site and flying in the direction of the open marshland.

Other species of Microchiroptera known from the area include *Emballonura atrata* (Emballonuridae), collected near the Marovony Forest (USNM 577062, 577063, 577257, 577258), north of Manantenina, and near Fanjahira, on the western side of the Vohimena Mountains (Peterson et al., 1995); *Triaenops rufus* (Hipposideridae), along the Itaranta River (USNM 577064), and near Tolagnaro (Peterson et al., 1995); *Miniopterus majori* (Vespertilionidae), at Manantantely (USNM 577075) and along the Itaranta River (USNM 577076–577078); and *Mormopterus jugularis* (Molossidae), near Tolagnaro (Peterson et al., 1995). Also, *Pipistrellus nanus* (= *Pipistrellus* sp., *sensu* Peterson et al., 1995) and *Miniopterus* (*minor*) *manavi* have been reported from the RNI d'Andohahela (Nicoll & Langrand, 1989).

Discussion

Over the past few years a number of bat inventories have been conducted in the eastern humid forests of Madagascar, and sufficient data are now available to permit preliminary comparisons between the faunas of these different sites. It must be noted that although the data from the RNI d'Andohahela, RNI d'Andringitra, and RS d'Anjanaharibe-Sud are comparable with respect to sampling effort (Goodman, 1996, 1998, herein), the species lists that were generated should not be considered complete. During these surveys no effort was made to employ canopy nets, which are useful for capturing high-flying species, nor were any searches made for roost sites (Voss & Emmons, 1996). Other chiropteran species will undoubtedly be found at these forest sites with further sampling. Even with these limitations, however, several clear patterns have emerged.

On the basis of faunal inventories, the forestdwelling bat community of the eastern humid forest of Madagascar shows low species richness and little species turnover across nearly the complete length of the island and nearly 12° of latitude (Table 15-2). The majority of bats classified here as forest-dwelling species also occur outside of this habitat, and they presumably forage in open areas.

Probably the most intensive survey of bats in the humid forests of Madagascar was conducted by Pont and Armstrong (1990) in the RNI de Marojejy, where 23 bats of eight species were captured in 8.071 net meter hr. Of this capture effort, 1,063 net meter hr (13% of the total) accrued in primary forest formations where not a single bat was captured. Although this reserve had more intensive sampling effort and higher species richness compared to the other three sites presented in Table 15-2, there are few differences among these four reserves in the forest-dwelling portions of their bat faunas.

Peterson et al. (1995) recognized 29 different bat species on the island. This figure includes species living in open areas, as human commensals, and in humid and dry forests. When compared to other large Old World tropical islands of similar surface area, such as Borneo and New Guinea (Payne et al., 1985; Flannery, 1990) the bat fauna of Madagascar is depauperate. In particular, there is no evidence of a distinct obligate forest-dwelling bat community on Madagascar. The use of harp traps or very fine mesh mist-nets during inventories might reveal a greater diversity of forest-dwelling bats than that demonstrated through the use of standard mist-nets.

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Literature Cited

- ANDERSEN, K. 1908. Twenty new forms of *Pteropus*. Annals & Magazine of Natural History, 8th series, 2: 361–370.
- BERGMANS, W. 1994. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera), 4: The genus *Rousettus* Gray, 1821. Beaufortia, 44: 79– 126.
- DORST, J. 1947a. Les chauves-souris de la faune Mal-

gache. Bulletin du Muséum National d'Histoire Naturelle, séries 2, **19:** 306–313.

- ------. 1947b. Essai d'une clef de détermination des chauve-souris Malgaches. Mémoires de l'Institut Scientifique de Madagascar, séries A, **1:** 81–88.
- ——. 1948. Biogéographie des Chiroptères malgaches. Mémoires de l'Institut Scientifique de Madagascar, séries A, **1**: 193–198.
- FLANNERY, T. 1990. The mammals of New Guinea. Robert Brown and Associates, Carina, Australia.
- GOODMAN, S. M. 1996. Results of a bat survey of the castern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 284–288. *In* Goodman, S. M., ed., A floral and faunal inventory of the castern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s. 85: 1–319.
- . 1998. Notes on the bats of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, pp. 223–226. In Goodman, S. M., ed., A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s. 90: 1–246.
- —, M. PIDGEON, A. F. A. HAWKINS, AND T. S. SCHU-LENBERG. 1997. The birds of southcastern Madagascar. Fieldiana: Zoology, n.s. 87: 1–132.
- GÖPFERT, M. C., AND L. T. WASSERTHAL. 1995. Notes on echolocation calls, food and roosting behaviour of the Old World sucker-footed bat *Myzopoda aurita* (Chiroptera, Myzopodidae). Zeitschrift für Säugetierkunde, **60:** 1–8.
- HULL, J. E. 1993. Long-fingered bats of the genus *Mini-opterus* (Chiroptera: Vespertilionidae) from Madagascar. Mammalia, **57:** 401–405.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, xvii + 374 pp.
- PAYNE, J., C. M. FRANCIS, AND K. PHILLIPS. 1985. A field guide to the mammals of Borneo. The Sabah Society, Sabah, Malaysia.
- PETERSON, R. L., J. L. EGER, AND L. MITCHELL. 1995. Chiroptères, vol. 84. Faune de Madagascar. Muséum National d'Histoire Naturelle, Paris, 204 pp.
- PONT, S. M., AND J. D. ARMSTRONG. 1990. A study of the bat fauna of the Réserve Naturelle Intégral de Marojejy in north-east Madagascar. Report of the Aberdeen University expedition to Madagascar 1989. Department of Zoology, University of Aberdeen, Aberdeen, 57 pp.
- RASOLOZAKA, I. N. 1994. Les micro-chiroptères, pp. 64–67. In Goodman, S. M., and O. Langrand, eds., Inventaire biologique Forêt de Zombitse. Recherches pour le Développement, Série Sciences biologiques, No. Spécial. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.
- SCHLIEMANN, H., AND B. MAAS. 1978. Myzopoda aurita. Mammalian Species, 116: 1–2.
- VOSS, R. S., AND L. H. EMMONS. 1996. Mammalian diversity in Neotropical lowland rainforests: A preliminary assessment. Bulletin of the American Museum of Natural History. 230: 1–115.